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"................. per litora spargite muscum,
Naiades, et circùm vitreos considite fontes:
Pollice virgineo teneros hìc carpite flores:
Floribus et pictum, divæ, replete canistrum.
At vos, o Nymphæ Craterides, ite sub undas;
Ite, recurvato variata corallia trunco
Vellite muscosis e rupibus, et mihi conchas
Ferte, Deæ pelagi, et pingui conchylia succo."
N. Parthenii Giannettasii Ecl. 1.

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I.—*On some Phenomena of the Development of the Organic Cell.* By Prof. H. Karsten*.

[Plate I.]

THE physics of the development and of the life of the cell, as the basis of all anatomy and physiology, constitute the first problem to be solved in both those sciences. Since Schwann declared that both animal and vegetable tissues consist of cells originally of a like nature, the similarity also in function of such cells both in animals and plants has been rendered more and more evident.

A clear perception of the whole of the physico-chemical phenomena which by their union constitute life will only be attained by an accurate knowledge of the origin and growth of the cell.

The formative elements of the cells which unite to constitute organic tissues have been largely investigated since the time when Robert Brown indicated the presence of a nucleus in numerous cells, and since I demonstrated that the cell-wall, previously regarded as a single sac, consists in reality of several endogenous superimposed laminæ (Karsten, De Cella vitali, 1843).

* Translated by Dr. Arlidge from a separate impression from Poggendorff's 'Annalen' (vol. cxviii., Berlin, 1863), for the communication of which we are indebted to the author.

The primary object at present is to determine the physical and chemical changes of the histological elements of cells during their development and multiplication, and, by the elucidation of these processes, to establish the laws which govern the origin and growth of an organ or of an organism, and which collectively make up the phenomena of life.

The most recent treatise on human histology, that by Kölliker (1862), refers to the purpose of the different histological elements of the cell, in respect both to its existence and its functions, thus:—1. The external wall of the cell serves only as a defence to its fluid contents (p. 39), except so far as it takes part in those intrinsic vital processes which are shown to occur by changes in its chemical constitution (p. 36); 2. the fluid cytoblastema pre-eminently constitutes the living portion of the cell (p. 39); and, 3. the cell-nucleus plays the most important part in cell-formation (p. 26).

This last proposition is advanced on the understanding that "the doctrine of free-cell formation in a cytoblastema has been set aside" (p. 28)—that cell-construction always coincides with cell-multiplication, being a result of the fission of a parent cell by means of the formation of folds in and the constriction or segmentation of its internal lamina (the primordial layer), although Kölliker fails not to remark that this process has, it is true, not yet been satisfactorily made out.

These fundamental doctrines of the histology of the animal body, which harmonize with the prevailing, but groundless, opinions upon the formation and function of the vegetable cell, have, however, not been confirmed in the vegetable organism with the clearness necessary for conviction. The history of development has rather proved that, in those cases (Karsten, *op. cit.* and Histologische Untersuchungen *, 1862) which have been cited as furnishing certain evidence of the multiplication of cells by segmentation, daughter cells, which originate freely in the fluid contents of the parent cell, cause the increase, and by their enlargement the division of the cell-interior by means of septa is brought about.

Moreover the wall of the cell is not simple, but composed of several cells placed one within the other, which are frequently regenerated from within outwards by the unfolding of the nuclear cell, and each of which cells passes through a course of development peculiar to itself.

The involution of the coats of the cell, in the few tissues where it has as yet been actually observed, does not give rise to

* A translation of these valuable investigations will appear in a future Number of the 'Annals.'

new cells, but is only a phenomenon passively accompanying cell-multiplication.

The so-called nucleus is a nuclear cell possessing the faculty of development, though frequently suppressed in the course of development, and near to or within which two or more new cells (cell-nuclei) may arise in order to carry on the multiplication of the individual cell in question. Mirbel taught, and Mohl coincided with his views, that the fission of the cell proceeded by the growth of centripetal septa, or of involutions of its wall, breaking up its contents into sections, the external surface of which became subsequently hardened into a firm lamina or special cell-wall; and side by side with, but partially opposed to, this theory of cell-formation based on imperfect observations Schleiden afterwards enunciated his peculiar views on the function of the "resting" nuclear cell—the cell-nucleus first observed by Robert Brown, which, in cells developing slowly, may be frequently met with.

These opinions of Schleiden regarding the signification of the nuclear cell became a great impediment to advancing the knowledge of cell-development. His followers entered so fully into the notion that the nuclear sac is the constant formative centre of the cell, exercising a catalytic effect upon its fluid contents, whereby it brings about the precipitation from the surrounding fluid of a pellicular deposit around itself, that even those who regard the whole organism as built up by repeated multiplication of the first ovum-cell, resulting, as Mirbel supposed, from centripetal involutions of the integument, consider this cell-nucleus as the starting-point in this mode of cell-multiplication.

This involution is assumed to proceed, in these nuclear cells, in the same way as in the parent cell-membrane itself, by constriction followed by division—each of the segments of the cell-nucleus deriving, by means of a folding and constriction of the inner lamina of its mother cell, a capacious envelope constituting the wall of a new cell.

This process of multiplication of the nuclear cell (cell-nucleus), however, no more takes place than that of the mother cell by constriction.

The so-called constrictions or segmentations of the cell-nucleus belong, in fact, to the same category as the so-termed germinating cells. These forms are produced by the excessive development of daughter cells in a feebly vegetating parent cell which is in course of destruction; whilst the partial septa or folds interposed between the endogenous cells are not so much centripetal growths as the result of a passive condition of the cell-wall at those parts. (The simultaneous growth of these septa with the endogenous cells is not indeed a matter of direct observation; on the other hand, their subsequent absorption has been observed in various instances.)

That a cell-nucleus is, as a rule, present in actively growing cells, and that in withered cells or in those in a resting-state it disappears, corroborates the statement derived from direct observation, that this nuclear cell possesses the property of development in itself.

Indeed the constant absence of nuclear cells in the normally detached cells of the epidermis of animals, and of the epithelium, in the cells of the tissue in the tail of the tadpole, in the woody cells of plants, &c., intimates the incapacity of such cells for further regeneration and individual development.

As only the resting-form of the nuclear cell in tissue-cells has hitherto been recognized as the cell-nucleus, in many cases the nucleus has been denied to exist where actually present and, indeed, in process of evolution, as, for instance, in tissues in continuous course of regeneration, *e. g.* in muscular tissue, the endogenous cells of which have at one time been considered nuclei, at another cells.

And it follows that, in cells which do not undergo regeneration as lasting tissue-cells, nor self-multiplication, the nucleus is always absent. Such cells are met with in those vesicles that are produced in connexion with secretions, and are to be found usually in large numbers in the fluid contents of genuine cell-tissue.

These generations of vesicles enclosed within a tissue-cell, and often engaged in constant formation and transformation, are the active instruments in the elaboration of organic material, transforming the inorganic matters dissolved in the cell-juices into combinations of a progressively higher grade. By means of the assimilative properties possessed by these simple cells, those substances are produced which either subserve the nutrition of the still assimilating membrane of the parent cell, or, where the cycle of its development is closed, are employed by the nucleus in the regeneration of the life-energy of the cell.

Moreover, when the individual development of the cell has ended, and, together with the nuclear cell suppressed in its revolution and destined to its regeneration, two or more new daughter cells are formed and developed at the expense of the parent cell, these secretory materials are employed for this purpose; and even after the formation of all such secondary generations is brought to a close, they are transferred by exosmose to other and remote parts of the organism to serve kindred purposes.

Some of these secretion-cells have walls so much thickened (*e. g.* starch), or such opake and solid contents (*e. g.* chlorophyll), that, for a long time, they have been looked upon, as some even now are, as solid unorganized particles; whilst others have such thin walls that they have either been overlooked, or else regarded as cavities in the less transparent and denser cell-contents.

Such gaps in our knowledge of the structure of the cell render the right apprehension of its functions impossible, as is shown, for example, among other problems, by that of the phenomenon of the circulation of the sap, which has been so much canvassed, and regarding which a distinguished physiologist has recently expressed himself in a manner which can only be explained by a misapprehension of the anatomical nature of the cell.

In my 'Histological Researches' (p. 61) I have detailed my views respecting the general cause of the circulation of the juices within cells; and I will now describe the structure of the hairs of *Urtica*, which explains the apparently wonderful circulation within their large cell-cavities. In Pl. I. figs. 1 & 2, is represented a large hair of *Urtica urens*, with its curved and rounded extremity. The large hair-cell, under a low magnifying power, appears filled with a colourless though somewhat turbid liquid, and has an inferior rounded extremity surrounded by an epidermic layer of cells. On the wall (as in fig. 1) or in the median line (in fig. 2) of the portion of the hair-cell which projects freely from the cup-like base is seen a large nuclear cell filled with a whitish mucilaginous substance and a nuclear vesicle. At times, particularly in fully grown stages, this organ is concealed by the cellular envelope at their base.

By rather stronger magnifying powers, it becomes evident that this nucleus is the central point of currents of a turbid finely granular fluid, which spreads itself more or less completely over the inner surface of the thick wall of the hair. By a little attention, it is further seen that the streams which pass across the interior of the cell are not all thread-like, as appears at first sight, or at least are not constantly so, but in part coalesce into a thin layer of fluid, which here and there, especially in the lower portion of the hair, gets collected in the form of a thicker column, usually more rapid in its course. The fibre-like stream is also as little constant in character as the wider but thinner current: at times it flows rapidly, at others slowly; at one time the tenacious-looking granular fluid collects in one place, at another it breaks away from the locality in which it has been confined, to extend to other parts, and thereby suffers some change in its direction. A rapid current is established especially after the hair has been placed in water under the microscope for a short time, as from two to three minutes, —a circumstance, no doubt, due to the diffusion of the water.

The circulation then proceeds for several hours, becoming weaker and weaker, until it at length entirely ceases, the fibres of the cloudy fluid growing more obscure, from an apparent coalescence within the interior of the cell.

The central nuclear cell, moreover, usually sank, during these phenomena, lower down in the cell; and the same organ, when attached to the wall, often showed also a slight change of place.

The largest portion of the upper extremity of the cell is usually divided, by only one obliquely directed stratum of circulating fluid, into two long sections; but its lower portion is broken up into several rounded clear spaces by shorter layers. In the interspaces formed by the contiguous borders of three such clear spaces, as also in the canals running along the wall of the cell, bounded by the adjoining sides of other two, circulate more rapidly the usually thicker, filiform and more visible threads.

Hence it is evident that the internal cavity of the thick-walled large hair-cell is subdivided into several hollow spaces, filled with a transparent homogeneous fluid, and that these spaces are capable of undergoing some change of form very gradually, and are separated from one another and from the external wall, more or less completely, by means of a system of mucous currents.

There also exist within the interior of the hair-cell, betwixt the spaces filled with homogeneous watery fluid, other spots unoccupied by the turbid matter in circulation; or such are seen to originate under the eye of the observer by a disintegration of the circulating substance. At such spots the larger clear spaces are therefore separated by very thin dissepiments. All these conditions bear testimony to the fact that the hair-cells of *Urtica urens*, and, in fact, many parenchymatose plant-cells, are occupied, at a certain stage of their development, by a tissue composed partly of non-nuclear cells (secretion-cells) which are separated from one another not by a firm but by a fluid intercellular substance. When such a hair-cell is moistened with water, imbibition takes place through the external wall, and the intercellular matter gets diffused, the more remote portions becoming intermingled with the more central. The process may be watched for hours, and the streams seen to set out, until at length the delicate diosmotic and, doubtless, assimilating membrane of the endogenous cell-wall becomes destroyed by the excessive imbibition of the water.

From this object, therefore, the physiologist might satisfy his problem of explaining the vital phenomena of the organism from its structure and from the physical and chemical changes taking place in it, without being compelled to have recourse to an inherent contractility not referable to these factors. The rotation of the cell-juices appears to be a mere phenomenon of diffusion, —endosmosis co-operating on the one hand, and the property of assimilation possessed by the enclosing cell-wall on the other, in a continuous act of intermixing the materials concerned.

Brücke's interesting experiments prove that, as the lightning shivers the strong oak, so an excessive electrical current shatters the delicate cells within the hairs of *Urtica*, and puts an end to the interesting phenomenon of the circulation of their fluid contents.

If the lower segment of the hair be deprived of its outer coat and opened, one or more of the delicate-walled cells which occupy this portion swell up and protrude, whilst the rest sink down from the apex into the space thus left vacant, and occupy it.

The extruded cells have frequently (Pl. I. fig. 3) cellular contents, not observable in those contained in the naked apical portion; they therefore belong to the category of true tissue-cells.

The circumstance that the integument of actual tissue-cells (particularly in the lower animal organisms) is frequently as delicate as the thin walls of the cells found within the hairs of the nettle, and that also in other tissue-cells (especially in the simplest plants) it is so thick, gelatinous, and transparent that it is difficult to trace their boundary, has more than once lately given rise to the idea that there may be naked cells (without walls), which are only mucous globules.

In my 'Histological Researches,' before referred to, I have enumerated several instances in which apparently deficient cell-membranes, notwithstanding their great tenuity, could be recognized with certainty.

In this respect the Confervæ possess a special interest; they offer peculiarly suitable conditions for making investigations respecting the structure and development of the cell, as they may be examined under the microscope whilst growth proceeds—an advantage unattainable in more complex plants or in animals.

In fact, in many species of these plants, their component (tissue-) cells, in the earlier phases of development, are so very thin and transparent that they are rendered appreciable only by a more attentive observation of the changes in form and position of the other and more solid cell-contents. The observer may likewise arrive at a more ready acquaintance with the origin and growth of cells by the comparative investigation of their development under different conditions of nutrition—experiments and observations which are indispensable also to the systematist; for a change of the conditions of nutrition alters not only the phenomena of the growth of cells, but also frequently the very form of the Alga itself, even when this has been accounted a specific character.

The cultivation of *Spirogyra* has proved to me that this plant, when liberally supplied with organic nitrogenous matter, generates new cells profusely, but that, if this nourishment be withheld, growth is limited to the cell-wall. This observation consequently shows that a deficiency of such organic nutritive supply promotes the centripetal involution of the cell-wall of *Spirogyra*, which in normal conditions of nutrition does not happen.

On the contrary, by a large supply of organic nitrogenous material, the growth of the cell-wall, relatively to the formation and evolution of new cells, remains in arrear. The cultivation of such species of *Spirogyra* as *S. Hornschuchii* shows this. The partition-walls (septa) of this plant, under normal conditions of development, immediately after their origin produce circular folds of a determinate size; and the tissue-cells (joint-cells) only proceed to produce new cells, after the septiform circular folds have acquired their normal dimensions. (Pl. I. fig. 4 *a*.) But this same species, when richly supplied with nourishment in the manner stated, presented in the same individual three, and sometimes four, or even five partition-walls, *without such circular folds*, and thus indicated that the thickening and further evolution of the cell-wall had been supplanted by an augmented development of cells.

The accelerated formation and development of new joint-cells was accompanied by a considerable increase in the deposit of chlorophyll. The successive spiral coils of this substance, which are normally separated from one another by intervals of about twice their width, approximated so closely frequently about the middle and at the extremities of the cell as to touch, and sometimes to overlap, each other at their edges, or, indeed, in their entire width; the spiral band being, relatively to the extension of the cell, disproportionately elongated (figs. 7 & 8).

In those instances where the layer of chlorophyll does not acquire such an excess above its usual length, its increase will nevertheless be indicated by a horizontal coil being substituted in place of the normal oblique one, in the centre of the cell, over the very delicate nucleus (fig. 4). This coil, at the commencement of the development of new joint-cells, loses the concave, furrowed character of its external surface, becomes pressed against the wall of the cell and fixed in its central position, as it appears, and as the further course of cell-development proves, by the production of the daughter cells, which grow up from the two opposite extremities of the cell, and extend themselves towards its middle line. These have, however, as yet such thin and delicate walls, that they are not themselves visible, but become evident only by the changes they produce in the disposition of the layer of chlorophyll, and by the action of diosmotic fluids. Moreover, the chlorophyll-deposit gravitates towards the centre of the cell, in the vicinity of the nuclear cell and the approximating ends of the two endogenous cells (figs. 9 & 10). According as the enlargement of the nuclear cell, the absorption of the chlorophyll, or the increase in size of the daughter cells prevails at this stage, the subsequent phenomena vary.

Within the nuclear cell two new cells originate, not by any constriction and segmentation of its membrane, but by new growth within its fluid contents, the nuclear vesicles of which become at the same time absorbed. These facts cannot be more readily verified than in the larger species of *Spirogyra*. (See Histological Researches, figs. 83–85.)

The nuclear cell of *S. Hornschuchii* and of allied species is so delicate and transparent that it cannot usually be clearly demonstrated without the addition of iodine (Pl. I. fig. 5). And as the two daughter cells (fig. 6) contained in it are also only rendered perceptible by this treatment, this species is therefore not suitable for the study of this histological element of the joint-cell.

The growth of the two daughter cells contained in the nuclear cell into new joint-cells, as observed in other *Spirogyræ*, does not appear to take place in *S. Hornschuchii*; for in this example it is only the daughter cells of the secondary cell which constitute new joint-cells, whilst the daughter cells of the tertiary cell (the cell-nucleus) enclosed between septum-building young joint-cells, proceed to grow into the little circular folds on the partition-wall.

The hypothesis I first promulgated in Wiegmann's 'Archiv' for 1843, on the origin of the cup-shaped circular folds of the septa, derives confirmation from the occurrence of such developmental phases as are seen in fig. 11, which, though, indeed, of rare occurrence, are sometimes encountered, particularly in cultivated plants.

In this example the middle portion of the septum projects in the form of a hemisphere from each aspect, instead of two circular folds. Between this extreme modification and the usual form every intermediate grade may be met with.

The precipitation of the chlorophyll on the nuclear cell is scarcely observable under the ordinary conditions of nutrition and development, and is probably connected with a general increase in the amount of chlorophyll deposited.

It not unfrequently occurs that three daughter cells are simultaneously developed in a single joint-cell of *Spirogyra*. In the joint-cells of *S. nitida* it is most decidedly seen that the new partition-walls are not produced by a fold of the membrane of the parent cell; for the several chlorophyll-laminæ or bands which are present, and completely coherent or continuous at first, overlie the septum which originates from the mutual apposition of the endogenous cells (fig. 13).

In fig. 15, a cell of *S. orthospira* is represented, in which the two daughter cells, *a, a* (covered by slender chlorophyll-vesicles, within the secondary cell *b*, which has been cautiously detached by diosmosis from the primary cell, by the addition of a weak solution of chloride of calcium), are in process of forming a new septum between themselves, and having the nuclear cell interposed. The formation of folds from the secondary cell (primordial sac) is evidently here not the cause of the septum in existence, though it be still incomplete with reference to the parent cell.

Fig. 16 exhibits the following stage of development of a joint-cell of the same individual, in which neither the two daughter cells nor the secondary cells could be detached by the same reagent from the wall of the mother cell, although the secondary cells of the daughter cells have become separated from the coats of their primary cells. These latter formed the still extremely delicate septum which divides the cavity of the mother cell into two portions. The secretory materials (chlorophyll, starch, &c.) are in this stage already enclosed within the secondary cells of the daughter cells, whilst in the previous phase, represented in fig. 15, they are still found within the secondary cells of the parent cell.

The process of absorption of the chlorophyll-vesicles contained within the mother cell, and their reproduction in the daughter cells, may be detected in this genus of plants, although not in its details; but in *Œdogonium* I have witnessed this process after the origin of new joint-cells.

These at first exceedingly delicate partition-walls, developed in a normal manner, can scarcely be confounded with the centripetal circular folds which the cell-membrane of badly nourished Confervæ, particularly *Cladophoræ* and *Spirogyræ*, not unfrequently produce; for these latter are much thicker, and their central edge always rounded, as is shown in figs. 12 & 14. In these examples, the membrane of the secondary cell which was detached from the thickened wall of the primary, as a result of diosmosis, at the constricted part at *x*, and which, during the operation of the reagent, was disturbed from its position, was free from chlorophyll. This nitrogenous secretory matter could not, from the deficiency of suitable nutritive material, develope itself proportionately with the growing cell-membrane, and, probably also from this same defect in the supply of nitrogenous substance from without, was absorbed by the more actively assimilating membrane of the fold.

In *S. nitida* I have observed such circular folds for fourteen days together, without being able to detect a further enlargement of them; and I can give so much the less credence to the hypothesis that septa and cells originate from these folds, as I have noticed similar circular folds in *Cladophora glomerata* lasting for a period of three months without any change in their central aperture taking place.

Further, I have not only observed, in *Cladophora,* the new joint-cells, in certain exceptional cases, take on such a development as to present two free endogenous cells dividing in the cavity of the mother cell (as in cork-cells, in *Spirogyra,* and *Œdogonium*: see my 'Histological Researches,' figs. 21–29), but I have also seen, in the plant in question, that the thick membranous folds intervening between the two daughter cells grow gradually thinner and become finally absorbed. In *Spirogyra,* moreover, I have also witnessed the absorption of the membrane of the secondary mother cell, which has subsided, along with the chlorophyll-vesicles connected with it, towards the conjoined ends of two slowly growing joint-cells, and has there become included in the septum produced, and assumed the form of an elevation or fold. (Histological Researches, p. 63.)

From the analogy of these occurrences, it may be assumed that even the folds represented in figs. 12 and 14 would become absorbed by the neighbouring cells, if these last were restored to a vigorous and normal state of nutrition, which might in all probability be effected, where atrophy had not too far advanced, by the cautious supply of organic nutritive matter.

Fig. 19 exhibits a specimen of *Cladophora glomerata,* in which one of the two daughter cells, during the absorption of the secreted matters by the fold, has penetrated this last in the course of its growth, come into contact with its sister cell, and thus established a new septum.

In the same plant (fig. 18) a thick fold has formed a boundary between the two new daughter cells, and so created an obstacle to their coming into apposition. In the centre of the fold a large corpuscle, like a starch-globule, remains unabsorbed by the daughter cells which did not touch it. It would seem that, in this example, the very thick circular fold of the mother cell has prevented the formation of a septum by the daughter cells.

A careful examination of *Cladophora* is sufficient to convince any one who might regard an appeal to analogy, even in allied plants, as inadmissible, that though an endogenous cell-growth is often difficult to discover in this plant, yet such is the fact; whilst the majority of naturalists, without it, acknowledging the general application of the law of analogy, will not suppose that, in the simplest processes of organization, nature follows totally different courses.

The primitive form which matter capable of organization assumes is that of the vesicle—the cell, inseparably composed of membrane (wall) and contents. Each of these two constituents of the elementary organ, constantly exerting the most intimate influences upon each other, is capable of advancing further in its development by the aid of the physico-chemical forces to which it is indebted for its existence.

The membrane of the cell grows, but not by passive extension as a consequence of endosmose of its fluid contents. It is rather itself engaged in a constant, although, in fact, almost imperceptible, change of the quantity and nature of the matter composing it, assuming peculiar forms, very probably dependent upon the nature of this material, as I have in some measure shown in the preceding pages and in several other contributions.

The fluid contents of the cell have also their own peculiar powers of development. Whilst the cell-wall shows this by its enlargement, and usually laminated thickening, the fluid contents manifest it by the production in them of secretion-cells, of transient duration.

Indeed, as the assimilative faculty of the cell-wall gives rise to the formation of progressively higher combinations, the soluble products of which become finally dissolved in the general nutritive fluid, so, by the agency of the same faculty, secretion-cells make their appearance in the fluid contents of tissue-cells at certain periods of their development. These transient secretion-cells serve for the maintenance of the cells of a secondary, tertiary, and succeeding generation, which originate in the cell-juices, are developed at the cost of the absorbed secreted matters, and serve for the reparation of the primary cell and the maintenance of the cell-individual. This formative process within the cell is not restricted, under certain conditions of nutrition, to the regeneration of the individual cell, but from the cell-contents rich in formative material several new cells, of the nature of the reproducing mother cell, are simultaneously produced, having for their object the multiplication of the tissue-cells.

Owing to this complicated structure of the tissue-cells which enter into the composition of developed organisms, it is erroneous to speak of unicellular plants and animals. With as little reason can we imagine cells without membranes; such bodies, in my opinion, should be designated drops or granules.